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RESEARCH ARTICLE

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Convergent evolution and convergent loss in the grasping structures of immature earwigs and aphidlion-like larvae as demonstrated by about 100-million-year-old fossils

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Abstract

Convergent evolution is a common phenomenon, independently leading to similar morphologies in different evolutionary lineages. Often similar functional demands drive convergent evolution. One example is the independent evolution of grasping structures in different lineages of Euarthropoda, though the exact morphology of these grasping structures varies significantly. In this study, we investigated grasping apparatuses with two movable counteracting structures as well as some related structures, exemplified by the stylets (compound structures of mouthparts) of aphidlion-like larvae (part of Neuroptera or lacewings) and the cerci of immature earwigs (Dermaptera). For the stylets of aphidlion-like larvae, studies have pointed to a significant loss in morphological diversity in the last 100 million years. We used quantitative morphology to evaluate if a similar process has also occurred in the cerci of earwigs. The cerci of extant immature earwigs exhibit two distinct types of morphologies in the modern fauna: elongated cerci divided into several ringlets with a feeler-type function, and pincer-like stout cerci. In some fossil immature earwigs, however, the cerci are generally elongated but undivided and roughly occupy the morphospace between those of the two modern cerci types; hence this fossil cerci morphology appears to have been lost. To some extent, a comparable loss is also found in certain lacewing larvae. Outgroup comparisons suggest that the morphologies no longer present today are in fact not ancestral, but instead specialised, hence their loss is possibly resulting from disruptive evolution in earwigs as well as lacewings. We discuss the possible functions of these specialised grasping structures.

Keywords Dermaptera, Neuroptera, Kachin amber, Myanmar amber, Cretaceous

Introduction

Convergence is the phenomenon that distantly related lineages evolve similar morphologies independently. The similarity may be on a purely functional level, as in the evolution of wings (in the groups Pterygota, Avialae, Pterosauria and Chiroptera; e.g., McGhee, 2011), or also on a level of appearance, concerning shape and colour, for example in cases of mimicry (Doyen & Somerby, 1974; Dumbacher & Fleischer, 2001; Elias et al., 2008; Franks & Noble, 2003; Haug et al., 2020a; Moynihan, 1968; Vane-Wright, 1980; but see Wickler, 2013). How similar the morphologies of two lineages have to appear to be considered a case of convergent evolution

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is sometimes a matter of debate (see discussion in Haug et al., 2020a), but approaches that can quantify similarity, such as quantitative morphology, can at least in part provide a conceptual frame for evaluating similarity (Baumgart et al., 2021; da Cunha et al., 2015; Thacker & Gkenas, 2019).

Grasping is an essential task for many representatives of Euarthropoda (Földvári et al., 2019), the group including, among others, beetles, spiders, crabs, and centipedes. Grasping may, for example, be important to catch and secure prey (Pazinato et al., 2021), to cling onto a host (Morand et al., 2000; Nagler & Haug, 2016), or also to hold onto a mating partner (Arnqvist, 1989; Arnqvist & Rowe, 2002; Thornhill, 1980). Grasping structures can, for example, be configured as true chelae as in lobster-type crustaceans (Elner & Campbell, 1981; Zhou et al., 2010; Fig. 1A) or scorpions (van der Meijden et al., 2010). In such an arrangement, a (rather) distal element of an appendage ("leg") forms a movable finger and can close against a protrusion of the next proximal element, functionally forming the fixed finger.

In another configuration, the distal element (or several of these) can fold against the next proximal one in a jackknife-like manner, representing a so-called subchela (Ass, 1973; Bruce, 1988). Such an arrangement is, for example, well known in praying mantises (Brannoch et al., 2017; Ramsay, 1990; Fig. 1B).

A less commonly recognised grasping configuration involves two movable structures, often entire appendages, which act against each other, resulting in a quite symmetric system that could be considered to have two movable fingers. This two-movable-fingers configuration is often found when the upper jaws (mandibles) are enlarged to grasp a prey item, as in predatory aquatic beetle larvae (Hájek et al., 2019; Michat & Torres, 2006), but also in trap jaw ants (Gronenberg, 1996; Larabee & Suarez, 2014; Patek et al., 2006;) and antlion(-like) larvae (Badano & Pantaleoni, 2014a; Badano et al., 2017; Fig. 1C), although in the latter each lower jaw or maxilla is functionally coupled to its corresponding mandible, forming a so-called stylet (MacLeod, 1964; Zimmermann et al., 2019). Another mouthpart-type example of a two-movable-fingers configuration is the lower lip of dragonfly and damselfly larvae (Büsse et al., 2017; Butler, 1904; Pritchard, 1965). Here, the two ancestrally feeler-like mechano-sensorial palps form the functional fingers (Fig. 1D).

Yet, there are also examples in which a similar configuration of a grasping apparatus is not formed at the anterior end, but at the posterior one. Examples are the grasping apparatuses of male dragonflies (e.g., Córdoba-Aguilar et al., 2015) or the cerci of earwigs. Many earwigs use their cerci, ancestrally also feeler-like mechano-sensorial structures (e.g., in the Jurassic in the group Protodiplatyidae; Grimaldi & Engel, 2005, Fig. 7.47; Zhao et al., 2010, Fig. 1; Zhao et al., 2011, Fig. 1a), as pincers (Simpson, 1993; Nishikawa, 2008; Országh et al., 2010; Fig. 1E). Pincer-type cerci may be used for different purposes (see also Briceño & Eberhard, 1995 and references therein):

1. Defence, i.e. to defend themselves (Eisner, 1960) or to defend a nest by females (Matzke & Klass, 2005, p. 107; Munoz & Zink, 2012, p. 944); this occurs also in immatures (Matzke & Klass, 2005, p. 102);
2. Catching prey, i.e. adults of some species have been observed to grasp prey with their cerci in oder to consume it (Matzke & Klass, 2005, fig. 1), being even able to subdue prey larger than themselves (Matzke & Klass, 2005, p. 102); this occurs also in immatures (Matzke & Klass, 2005, p. 102);
3. Unfolding wings (Haas, 2003);
4. Sexual interactions: in courtship (Walker & Fell, 2001); male-male competition (Tomkins & Simmons, 1996, p. 755); there might also be a female-choice component preferring certain cerci shapes (Rantala et al., 2007, p. 510).

Still, in few modern earwigs (in the groups Diplatyidae and Karschiellidae) the immatures possess feeler-like cerci. They gain pincer-like cerci when moulting to the adult (e.g., Shimizu & Machida, 2011, p. 84).

Besides the examples mentioned, the function of cerci of extant earwigs needs to be inferred from functional morphology to a certain extent as there are no comprehensive behavioural data available over all earwigs. Hence, the situation is similar to that in most fossils. We assume that most feeler-like cerci are used for mechano-sensorial purposes, while pincer-like cerci are used to grasp.

It appears that in numerous lineages, especially of Pterygota (the "flying insects", although many do factually not fly), grasping apparatuses with two movable fingers have evolved. These systems can be explored for further aspects of convergence. Not only antlions, but also many larvae of their relatives (collectively known as lacewings) have the special arrangement of their mouthparts for prey catching (MacLeod, 1964; Zimmermann et al., 2019). Qualitative and quantitative comparisons have demonstrated that the diversity of the morphology of the prey catching apparatuses of lacewing larvae, the head with stylets, has decreased in morphological diversity over time (Haug et al., 2019a, 2019b, 2020b, 2021a, 2022a, 2023a). In other words, there have been morphologies, i.e. specific types of (supposed) grasping apparatuses, in the past, which are now extinct.

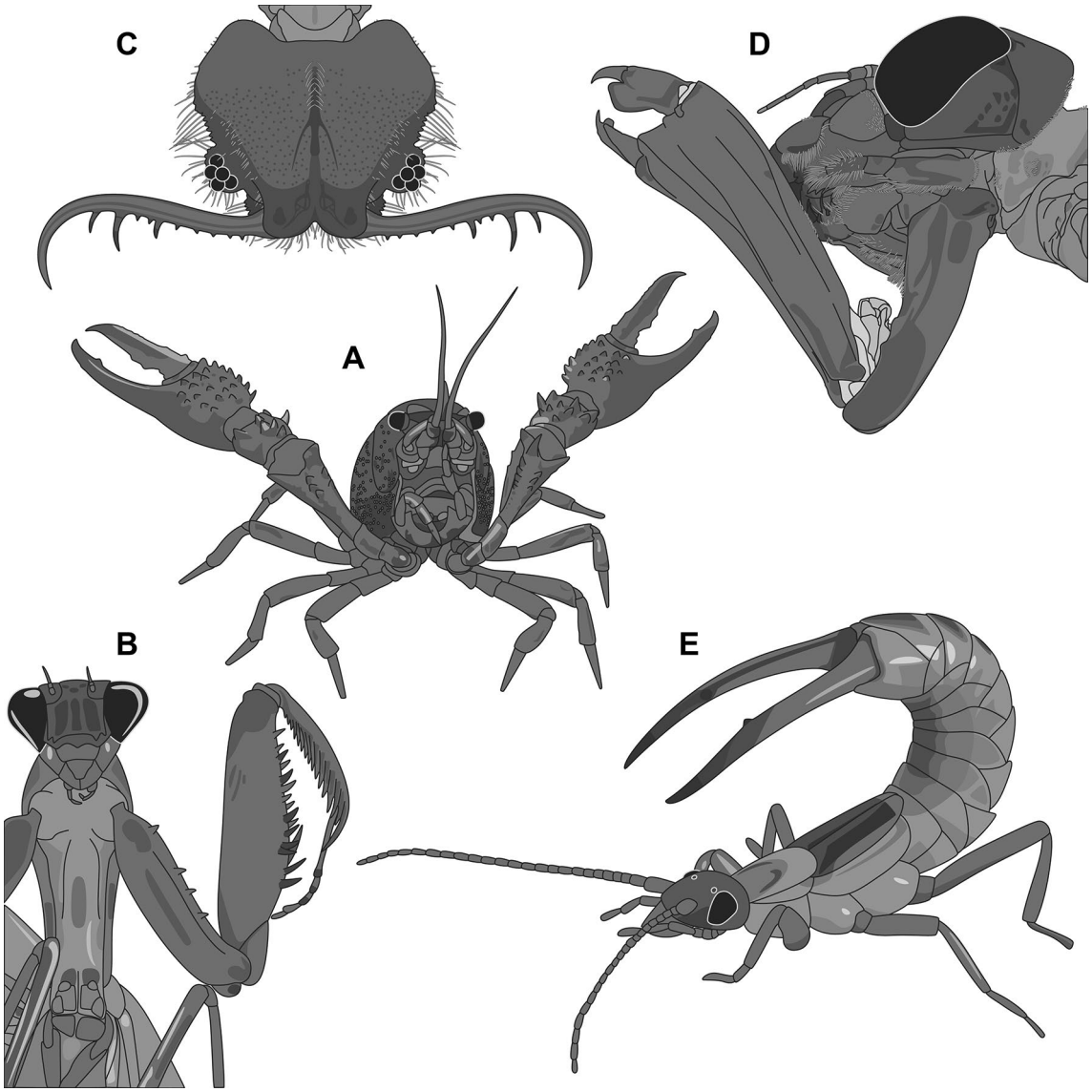

Fig. 1 Examples of representatives in Euarthropoda with grasping structures. **A** Red swamp crayfish *Procambarus clarkii* (Decapoda: Astacidae), anterior view, with chela, one-fixed-finger-one-movable-finger configuration; simplified after Kranking (2018, pp. 6–7). **B** Anterior body of praying mantis *Hierodula transcaucasica* (Dictyoptera: Mantodea), ventral view, with sub-chela, jackknife configuration; simplified after Ehrmann and Borer (2015, Fig. 35 right, p. 257). **C** Head of larva of an owllion (Neuroptera: Myrmeleontiformia), dorsal view, two-movable-fingers configuration of the mouthparts (stylets); based on specimen ZMH 62882 (collection of the Centrum für Naturkunde (CeNak), Leibniz-Institut zur Analyse des Biodiversitätswandels (LIB), Hamburg). **D** Head of a dragonfly larva (Odonatoptera: Odonata), ventro-lateral view, two-movable-fingers configuration of the palps of the labium ("mask"); simplified after Haug (2020, Fig. 4, p. 182). **E** Earwig (Polyneoptera: Dermaptera), dorso-lateral view, two-movable-fingers configuration of the cerci; simplified after Országh et al., (2010, fig. on title page)

We here explore if we can recognise a similar pattern in earwigs, i.e. whether there were morphologies of the (supposed) grasping apparatus in earwigs in the past that are not found in the modern fauna. We quantitatively and qualitatively compare them also to the apparatuses in lacewing larvae to see whether comparable types of morphologies went extinct (see also comparison of earwig cerci with mouthparts of a beetle larva by Munoz & Zink, 2012, p. 944).

Material and methods

Material

The study made use of data from the literature (details in Additional file 1: Table S1 and Additional file 2: Text S1) and an earlier published data set (Haug et al., 2022b).

In addition, nine new specimens of fossil earwigs have been documented for this study. The new specimens are preserved in Cretaceous Kachin amber from Myanmar. They have been legally purchased over the platform ebay.com from the trader burmite-miner. The specimens are deposited in the collection of the Palaeo-Evo-Devo (PED) Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München (LMU Munich), Germany, under repository numbers PED 0016, 0132, 0170, 0956, 1506, 1510, 1532, 1538, and 1542.

It has been suggested that trading with amber from Myanmar plays a role in the military conflict within the country (recently reviewed by Dunne et al., 2022) and that a moratorium of working on this material would help to solve the issue, especially put forward by the Society of Vertebrate Paleontology (Rayfield et al., 2020). Yet, this suggestion is based on a rather one-sided view of (mostly) vertebrate palaeontology. Other palaeontologists have provided a different or more nuanced view on the topic (e.g., Haug et al., 2020c; Peretti, 2021; Shi et al., 2021). Also the idea that Myanmar amber has a direct influence on the conflict within the country has been questioned (Poinar & Ellenberger, 2020; but see discussion in Dunne et al., 2022).

The more recent ideas of how to document export processes from Myanmar (Theodor et al., 2021) may be applicable to expensive vertebrate fossils, but according to trader information and own experiences, pieces of few dollars of value will not receive separate export papers. In our publications, we are providing all information available to us about the provenance of the specimens for a maximum of transparency.

Another issue discussed in recent time is that of involving local people into research (to avoid the so-called "helicopter science" or "parachute science"; e.g., Stefanoudis et al., 2021; Zin-Maung-Maung-Thein & Zaw, 2021). We have successfully established a collaboration with biologists from the University of Yangon, Myanmar, in order to improve this aspect and recently published the first paper resulting from this collaboration (Haug et al., 2023b).

Documentation methods

New specimens were documented on a Keyence VHX-6000 digital microscope under different settings to achieve images providing maximum information (see details in Haug et al., 2019a, 2019b, 2019c).

Quantitative morphological analysis

Outlines of mouthparts, more precisely stylets, of lacewings larvae and outlines of cerci of earwigs were redrawn manually with a vector graphics program (Inkscape; Adobe Illustrator). For a uniform appearance of the non-accessible proximal parts, a simple half circle was added to the base (van der Wal & Haug, 2020). In case of flexible structures, for example due to joints, these were digitally straightened to reduce the influence of the posture. Only one side was used, the better accessible one.

Outlines were loaded into the free program SHAPE, transformed via Elliptic Fourier transformation and analysed via PCA (see Haug et al., 2020b, 2022a). Scatterplots were made in OpenOffice and redrawn in Adobe Illustrator CS2.

Two different data sets were analysed. Data set 1 includes only cerci of earwigs, in total 269. Data set 2 includes stylets of lacewing larvae, more precisely of aphidlions and aphidlion-like larvae (Chrysopidae, Hemerobiidae, and fossil relatives; see discussion in Haug et al., 2022b), as well as cerci of immature earwigs. This data set includes 400 outlines.

Setting a comparative frame

The aim of the study is to compare different structures in distantly related lineages which are considered functionally comparable. This approach therefore involves the comparison of the stylets (compound structure of upper and lower jaw) of lacewing larvae and the cerci of earwigs. These structures are clearly not corresponding to each other concerning segment identity (appendages of post-ocular segments 3 and 4 in lacewings, those of post-ocular segment 19 in earwigs) or leg element identity (coxa or basipod in lacewings, possibly exopod in earwigs; see discussion in Hädicke et al., 2014). Still, as outlined above, both structures can be moved against their counterpart to grasp, for example, a prey item. While there are differences in details (e.g., lacewings pierce their prey items, earwigs do not), the basic mechanics concerning lever and muscle force transmission are the same in both systems (yet there are exceptions in both groups where cerci or stylets are not used for grasping, see discussion for details). A common observation for supposed cases of convergence is that it is possible to mistake representatives or isolated structures of the one lineage for those of another one. Fragmented specimens preserved in amber indeed nicely demonstrate that the head of a lacewing larva can be mistaken for the trunk end of an earwig (personal observation of the authors). We therefore consider this comparison as useful in the outlined frame (see also Hammer, 2016 or Evans et al., 2021 for comparisons of the shape of very different structures).

Results

Short description of new specimens

The new specimens are here not treated in a detailed taxonomic frame and are only identified as immatures of the group Dermaptera. Further reaching taxonomic

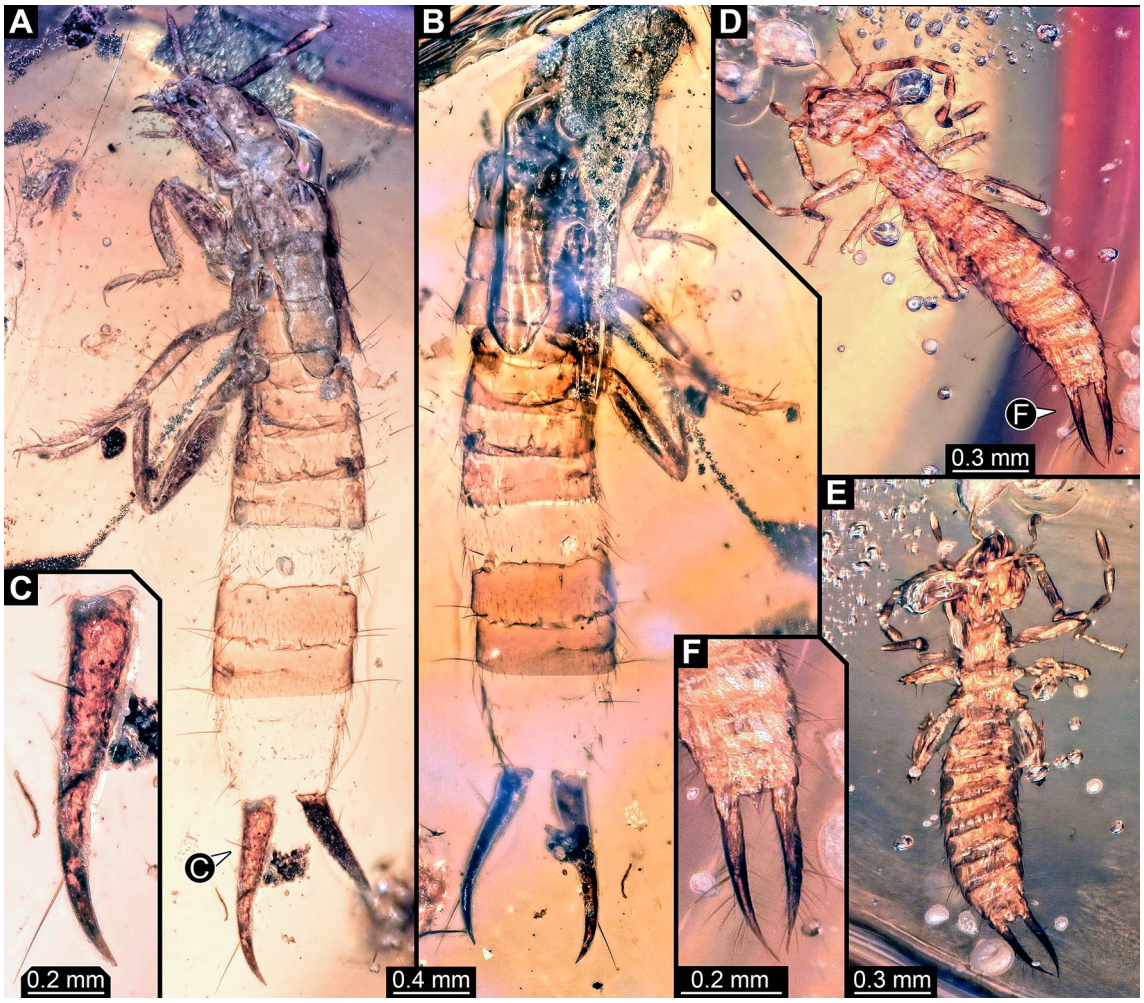

Fig. 2 New fossil immature specimens of Dermaptera, Myanmar Kachin amber. **A–C** PED 0016. **A** Ventral view. **B** Dorsal view. **C** Close-up on cercus. **D–F** PED 0132. **D** Dorsal view. **E** Ventral view. **F** Close-up on cerci

interpretations are challenging, as the specimens are immatures and furthermore often lack access to diagnostic features. They are treated here as they offer access to the shape of the cerci, which is the central structure of interest for this study.

(1) *Specimen PED 0016:* The specimen is accessible in ventral (Fig. 2A) and dorsal view (Fig. 2B). The cerci (Fig. 2C) are pincer-like.
(2) *Specimen PED 0132:* The specimen is accessible in dorsal (Fig. 2D) and ventral view (Fig. 2E). The cerci (Fig. 2F) are pincer-like.
(3) *Specimen PED 0170:* The specimen is accessible in dorsal view (Fig. 3A, B). The cerci are not subdivided, thin, elongated and gently inward curved (Fig. 3C).
(4) *Specimen PED 0956:* The specimen is accessible in dorsal (Fig. 3D) and ventral view (Fig. 3E). The cerci (Fig. 3F) are more robust, but still elongated, almost straight, only inward-curving distally.
(5) *Specimen PED 1532:* The specimen is accessible in ventral view (Fig. 4A). The anterior part of the specimen is not preserved. The cerci are rather short, robust, slightly inward curved.
(6) *Specimen PED 1506:* The specimen is accessible in dorsal view (Fig. 4B). The cerci are rather short, almost straight (Fig. 4C).
(7) *Specimen PED 1510:* The specimen is accessible in dorsal(?) view (Fig. 4D). The cerci are very long, almost straight only slightly inward curved.
(8) *Specimen PED 1542:* The specimen is accessible in dorsal (Fig. 5A) and ventral view (Fig. 5B). The cerci are very long and appear subdivided into several elements (Fig. 5C).
(9) *Specimen PED 1538:* The specimen is accessible in ventral view (Fig. 5D). The cerci are elongated,

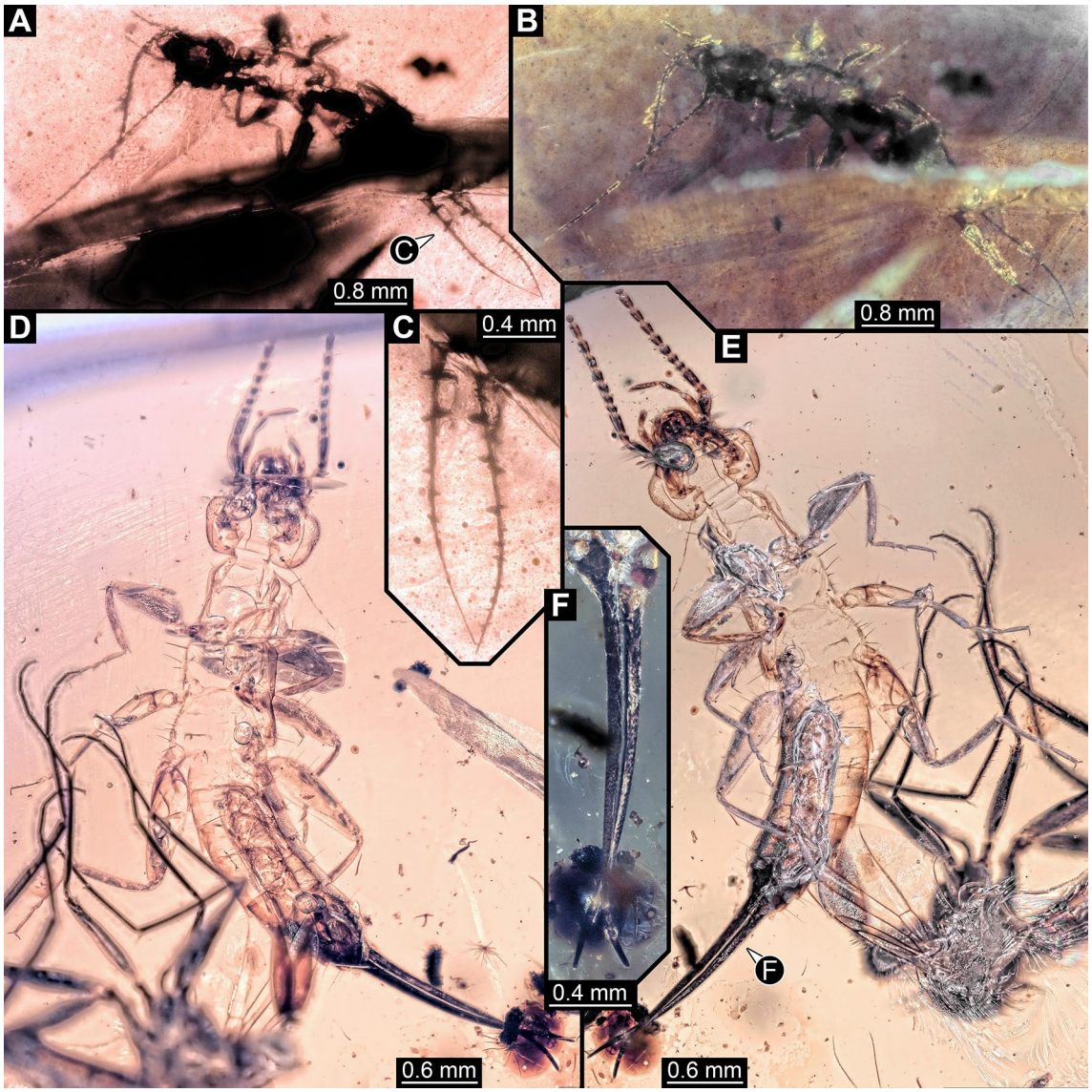

Fig. 3 New fossil immature specimens of Dermaptera, Myanmar Kachin amber, continued. **A–C** PED 0170. **A**, **B** Dorsal view under different light settings. **C** Close-up on cerci. **D–F** PED 0956. **D** Dorsal view. **E** Ventral view. **F** Close-up on cerci

straight and appear not subdivided into several elements (Fig. 5E).

Analysis of cerci of earwigs

The PCA resulted in five effective PCs. For details of the analysis, see Additional file 3: Text S2 and Additional file 7: Files 1–5.

PC1 explains 65.50% of the overall variation. It is dominated by the type of curvature. Low values indicate an S-type of curvature, proximally outward curving and distally inward curving. High values indicate a strong inward curvature distally (Additional file 5: Fig. S1).

PC2 explains 14.11% of the overall variation. It is dominated by the curvature of the proximal and distal region. Low values indicate a proximal inward curving and straight distal region. High values indicate proximal outward curvature and a distal inward curvature (Additional file 5: Fig. S1).

PC3 explains 7.36% of the overall variation. It is dominated by the position of the distal curvature. Low values indicate a further distal inward curvature. High values indicate a further proximal inward curvature (Additional file 5: Fig. S1).

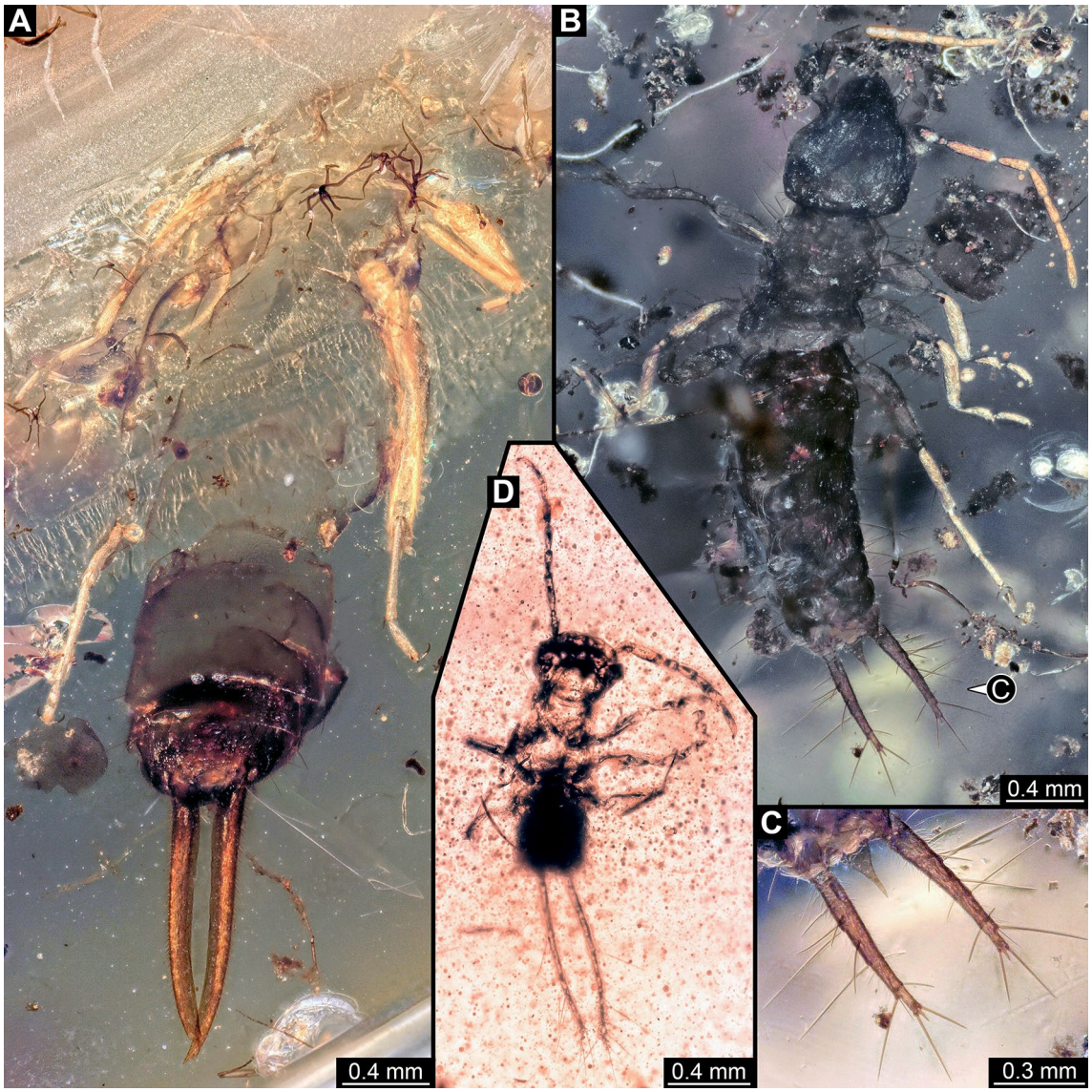

Fig. 4 New fossil immature specimens of Dermaptera, Myanmar Kachin amber, continued. **A**. PED 1532, ventral view. **B, C**. PED 1506. **B**. Dorsal view. **C**. Close-up on cerci. **D**. PED 1510, dorsal(?) view

PC4 explains 3.75% of the overall variation. It is dominated by the position of a slight constriction between proximal and distal region. Low values indicate a further distal position. High values indicate a further proximal position (Additional file 5: Fig. S1).

PC5 explains 2.95% of the overall variation. It is dominated by the position of the distal curvature. Low values indicate a further proximal inward curvature. High values indicate a further distal inward curvature (Additional file 5: Fig. S1).

Analysis of cerci of immature earwigs and stylets of lacewing larvae

The PCA resulted in three effective PCs. For details of the analysis, see Additional file 4: Text S3 and Additional file 8: Files 6–10.

PC1 explains 85.42% of the overall variation. It is dominated by overall curvature. Low values indicate an almost straight structure. High values indicate a strongly curved one (Additional file 6: Fig. S2).

PC2 explains 6.81% of the overall variation. It is dominated by the relative position of the curvature. Low values indicate a further distal position of the curvature.

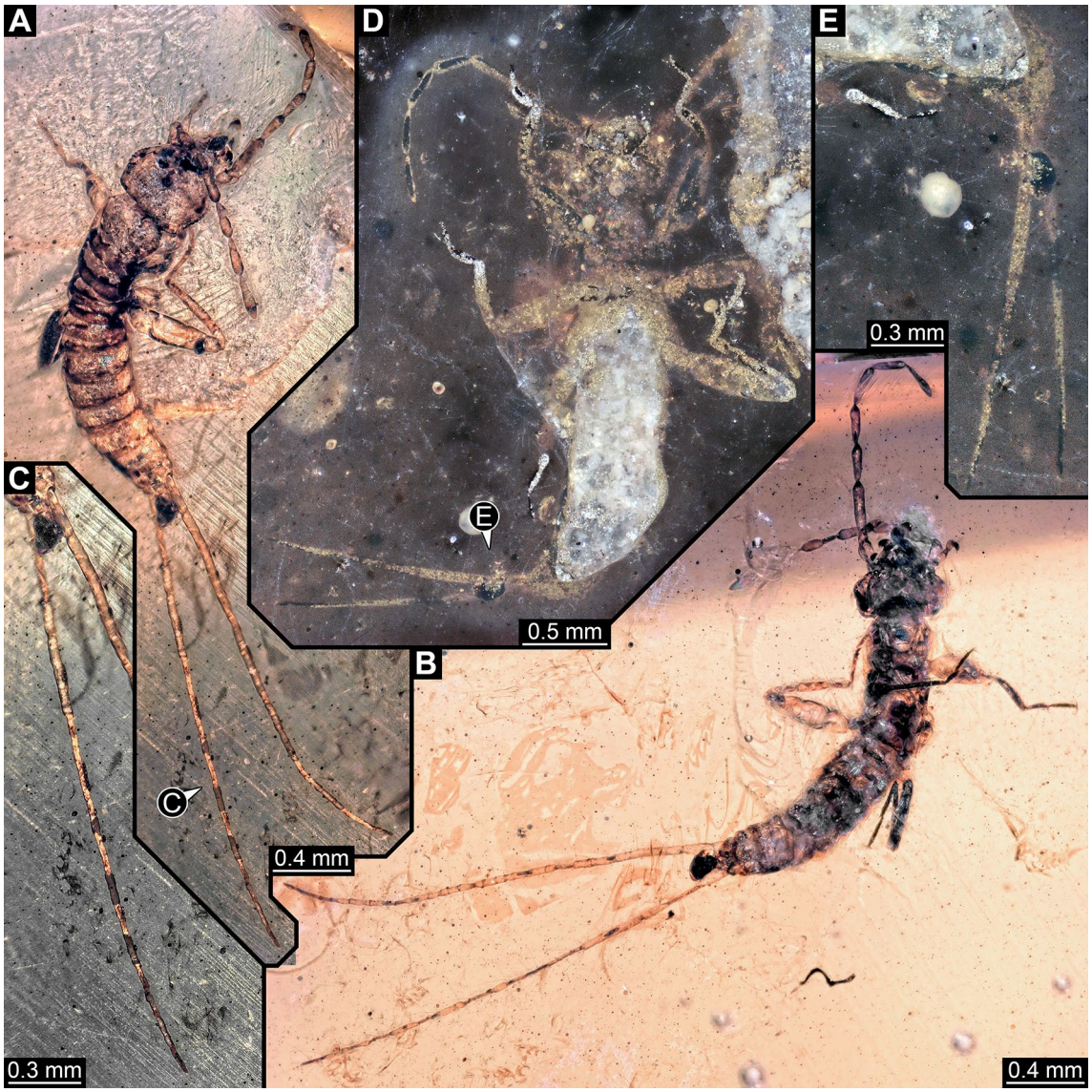

Fig. 5 New fossil immature specimens of Dermaptera, Myanmar Kachin amber, continued. **A–C** PED 1542. **A**. Dorsal view. **B** Ventral view. **C** Close-up on cerci. **D, E** PED 1538. **D** Ventral view. **E** Close-up on cerci

High values indicate a further proximal position of the curvature (Additional file 6: Fig. S2).

PC3 explains 2.82% of the overall variation. It is dominated by the distal curvature. Low values indicate a slightly straighter tip. High values indicate more curved tip (Additional file 6: Fig. S2).

Discussion

Restrictions of the comparisons

We restrict the comparison here to immature earwigs as the diversity of adult cerci in earwigs is apparently strongly driven by sexual selection, which leads to a very wide morphospace occupation especially in adult males (Fig. 6). Such selective pressures are clearly absent in lacewing larvae. To eliminate the sexual selection effects, restricting selective pressure on functional aspects, focussing the comparison to immatures seems the most effective strategy (Fig. 7). The downside of this strategy is that there is far less data available for immature earwigs than for adults, strongly reducing the sample size. Yet, an advantage of this restriction is indeed that many fossil earwigs preserved in amber, which provide a very good preservation, are also immatures, making the data set more balanced in this aspect.

We also restricted the data set on the lacewing side. Many lacewing larvae have stylets that differ strongly in

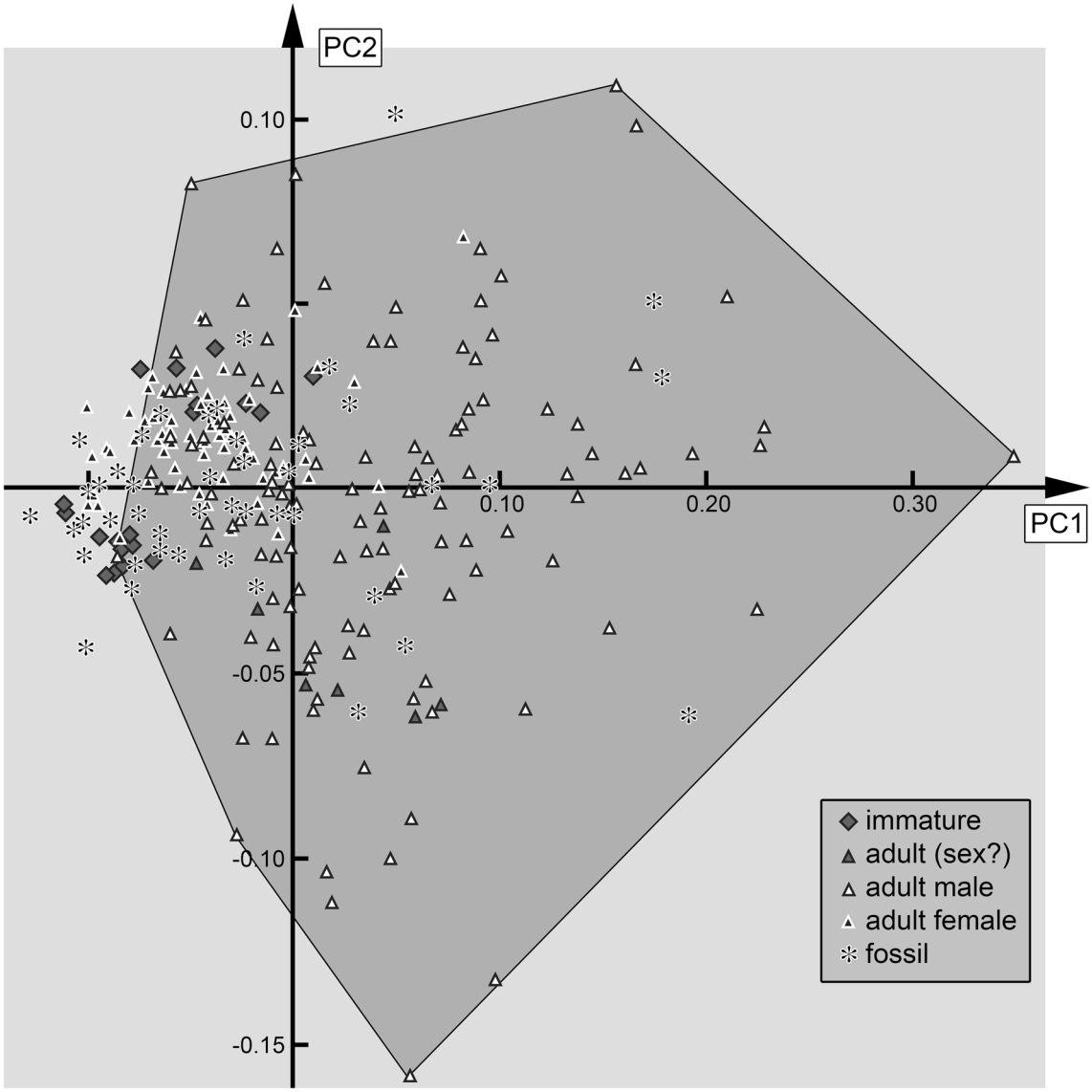

Fig. 6 Scatterplot of the first two principal components describing the outlines of the cerci of extant and fossil earwigs. Note that the largest part of the morphospace is occupied by adult males. *PC* principal component *sex?* sex unknown

shape from the cerci of earwigs, for example in possessing massive teeth as in antlion larvae (Badano & Pantaleoni, 2014a, 2014b; Badano et al., 2017) or in being straight (Haug et al., 2021b). Especially the latter configuration, as in larvae of Mantispidae (mantis lacewings), would not facilitate a good comparison, as here the mandibles are often not even movable any more (Jandausch et al., 2018), diluting the argument of comparable forces acting in both cases. We decided to use aphidlions and aphidlion-like fossils as a basis. These larvae represent a specific, most likely rather ancestral type of larval morphology (Haug et al., 2022b), which is well represented in the modern fauna, but also in the Cretaceous (Liu et al., 2016, 2018, 2022; Haug et al., 2022b; Pérez-de la Fuente et al., 2012, 2018, 2019; Wang et al., 2016). Also the stylets are rather simple in shape and appear qualitatively comparable to earwig cerci.

Loss of earwig morphology

The modern earwig immatures plot in two distinct clusters, with quite some distance between them (Fig. 8). Immature earwigs that plot in the upper left region of the plot have very elongated cerci, which are subdivided into numerous ringlets, giving it an overall feeler-like appearance. Such immatures will break off the cerci in their last immature stage (Shimizu & Machida, 2011); such

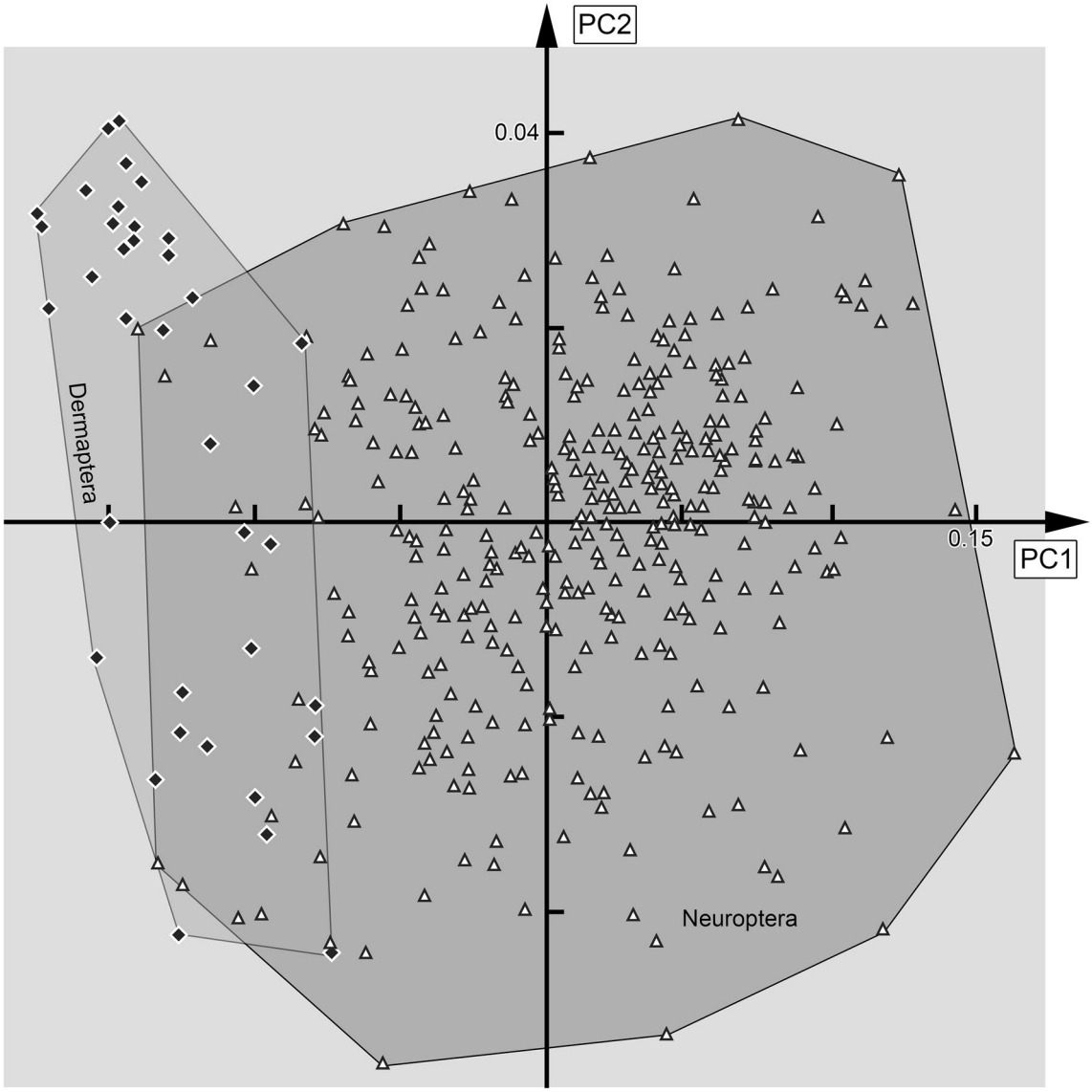

Fig. 7 Scatterplot of the first two principal components describing the outlines of grasping structures of only immature specimens, namely of earwig cerci and of aphidlion(-like) lacewing stylets. *PC* principal component

"broken-off morphologies" plot also close to the elongated ones. Adult representatives of these species have "proper" earwig-type pincers. Though one might argue that we should not consider the "broken-off morphologies" here as they do not operate as functional structures, we decided to include the entire range of morphologies of immatures; removing these might incorporate more unwanted subjectivity to the study. Other immature earwigs plot more in the lower left, possessing morphologies well known for adult earwigs, with cerci also forming prominent pincers.

The fossil earwigs plot, roughly, between these two types of modern morphologies (Fig. 8). These cerci are much more elongated and thinner than in the lower modern group (e.g. Nel et al., 2003, Fig. 6B; Engel, 2009, Fig. 1; Engel et al., 2011, Fig. 3; Engel & Perrichot, 2014, Fig. 1; Ren et al., 2018; Fig. 3D, 4D). Yet, unlike in the upper modern group, the cerci are not subdivided into ringlets, but form a single continuous structure. This specific type of morphology appears to be not represented in the modern fauna, at least not by immature earwigs, and is therefore considered lost or extinct in the modern fauna.

The plot may provide the impression of this fossil morphology to represent a kind of transitory one. One could get the impression that the evolutionary transition from

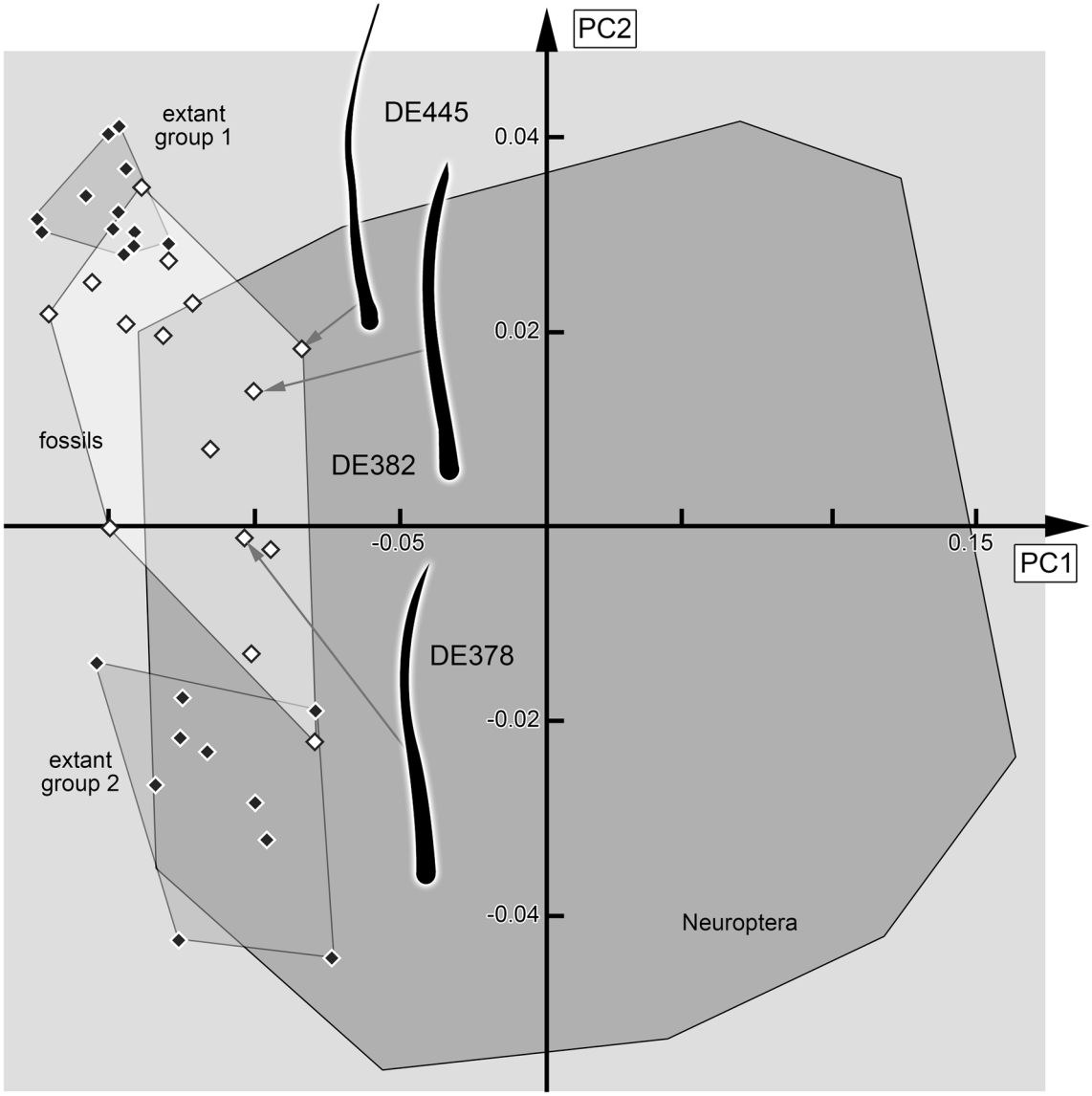

Fig. 8 Scatterplot of the first two principal components describing the outlines of grasping structures of only immature specimens, namely of earwig cerci and of aphidlion(-like) lacewing stylets. In contrast to Fig. 7, the cerci of extant and fossil earwigs are highlighted, with the extant ones plotting in two separate groups. Three example shapes of cerci of fossil earwigs are presented. *PC* principal component

a long subdivided cercus to a continuous short one could have looked similar to the fossil morphology. Yet, this is not backed up by the ontogenetic transition known from modern earwig immatures with long feeler-like cerci (which are presumably not used for grasping). There is no secondary fusion of elements to a continuous structure, but a breaking off of the distal part (also "fusion" seems an uncommon phenomenon in comparison to "not separating"; cf. Haug et al., 2009 vs. Haug et al., 2016). This consideration makes it more likely that the morphology of the fossils indeed represents a specialised rather than an ancestral type of morphology.

No such loss in aphidlions?

Aphidlions are spread more over the plot than are earwigs (Figs. 7, 8). This should not be to surprising given also the larger sample size. There are some extant aphidlions and fossil aphidlion-like larvae, which plot in the area of the fossil earwig larvae. On a first glance this indicates that this morphology, now extinct in earwigs, was in the past present in aphidlion-like larvae, but is also still present in aphidlions today.

Yet, here we additionally need to consider some other characters, not represented by the shape analysis. As PC1 is dominated by the overall curvature of the structure and

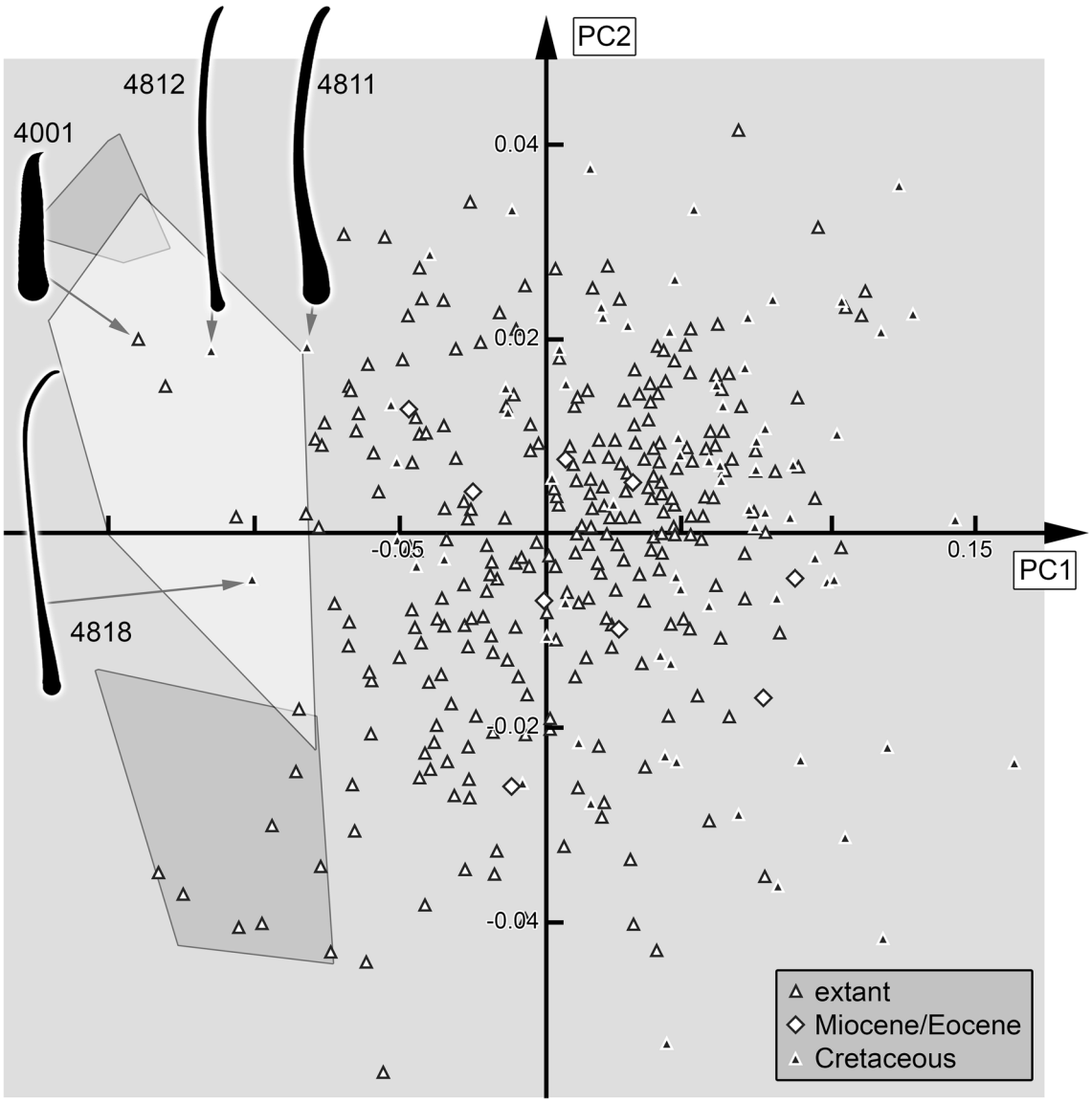

Fig. 9 Scatterplot of the first two principal components describing the outlines of grasping structures of only immature specimens, namely of earwig cerci and of aphidlion(-like) lacewing stylets. In contrast to Fig. 8, the morphospace occupation of the cerci of extant and fossil earwigs is only indicated by polygons. Three example shapes of fossil aphidlion-like larvae (4811, 4812, 4818) and one example shape of an extant aphidlion larva (4001) are presented. *PC* principal component

PC2 by the relative position of the curvature, there is no direct representation of the slenderness of the structure. As pointed out, the cerci of the earwigs in the Cretaceous are continuous, slender, and elongated (Fig. 8). Also the stylets of the fossil aphidlion-like larvae plotting in the same area are slender and elongated (Fig. 9). The stylets of the extant aphidlion larvae, on the contrary, are not especially elongated and slender (Fig. 9). In overall appearance, they are more comparable to the broken-off cerci of some of the modern earwig immatures. Hence also here we can recognise a comparable loss of morphology as in earwigs: elongated, slender, only mildly curved structures have been present in immatures of both lineages in the past, but are absent today (Fig. 10).

More distantly comparable losses

The "loss of slenderness" seen in immature earwigs and aphidlion-like larvae in the analysis can also be recognised qualitatively in other examples. A unique aphidlion-like larva from Kachin amber performing mimicry (Liu et al., 2018; Li et al., 2022) could not be included into the quantitative analysis as the very proximal part of the

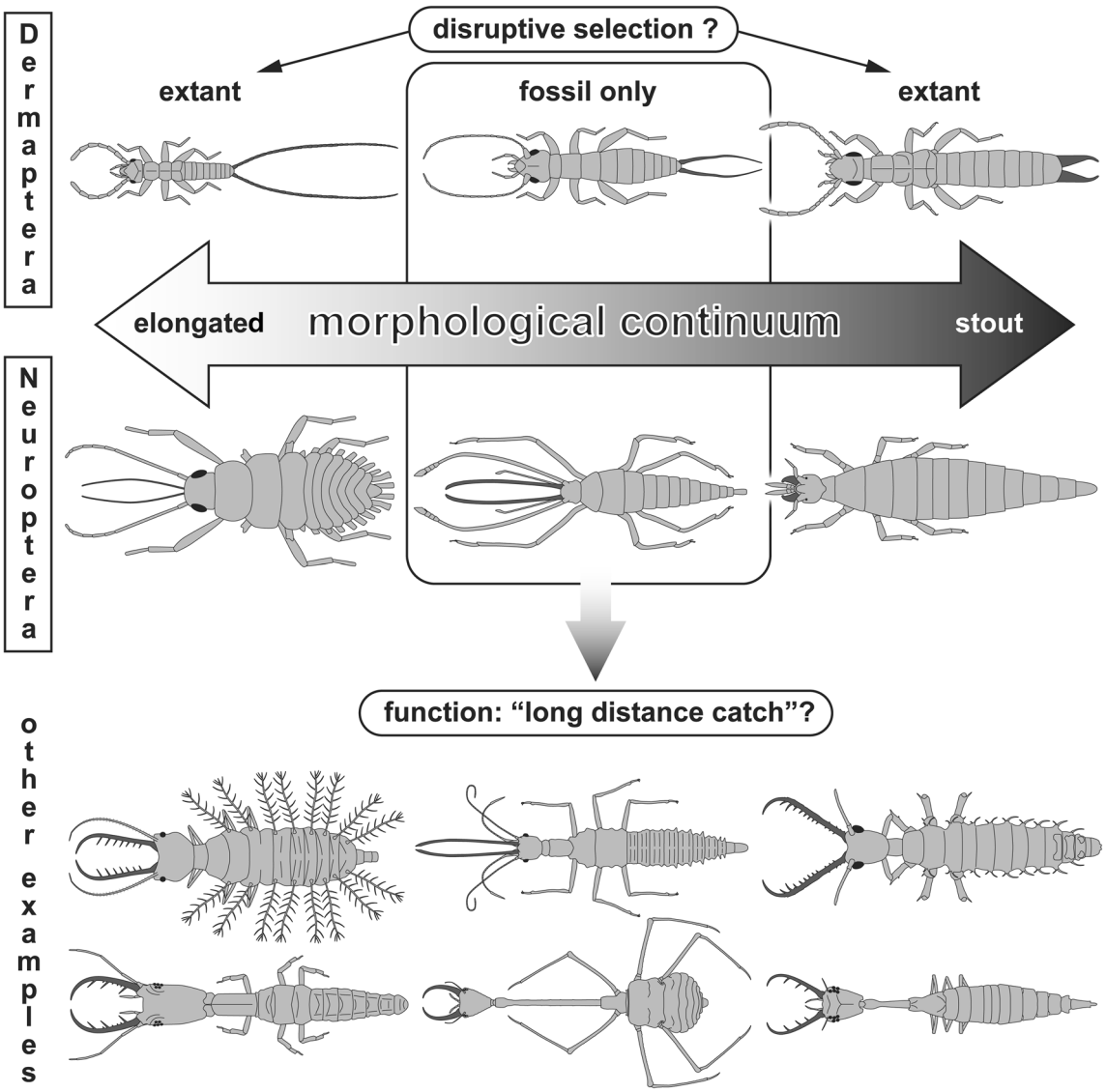

Fig. 10 Comparison of grasping structures of immatures of Dermaptera and Neuroptera. Top row and middle row: Corresponding shapes of cerci in Dermaptera (top) and stylets of Neuroptera (middle); specimen pairs in same column in top and middle row share similar principal morphology. Left, top row and middle row: Very elongated, slender and flexible morphology, seen in the modern fauna. Left, top row: Extant hatchling of *Diplatys flavicollis*; simplified after Shimizu and Machida (2011, Fig. 1C, p. 85). Left, middle row: Larva of *Sisyra iridipennis* (Sisyridae); simplified after Morales (2020, pl. 1B, p. 31). Middle, top row and middle row: elongated, but inflexible morphology as seen in the Cretaceous, but now extinct. Middle, top row: Fossil immature, based on specimen PED 0170 (see Fig. 3A–C). Middle, middle row: Fossil immature, specimen 4812; simplified after Zhang (2017, upper image on p. 384). Right, top row and middle row: Stouter morphology, seen in the modern fauna. Right, top row: Extant immature of *Euborellia arcanum*, specimen DE 261; simplified after Matzke and Kočárek (2015, Fig. 11 in image/Fig. 12 in caption, p. 135). Right, middle row: Larva of Hemerobiidae, based on specimen 4065. Bottom rows: Other examples of larvae of Neuroptera with elongated structures supposedly allowing for a long-distance catch; from upper row left to bottom row right: *Cladofer huangi*, simplified after Badano et al., (2018, suppl. Figure 1d, suppl. p. 10); "supersting larva", simplified after Haug et al., (2021a, Fig. 3A, p. 5); "superfang larva", simplified after Haug et al., (2019b, Fig. 3B, p. 438); *Macleodiella electrina*, simplified after Badano et al., (2018, Fig. 3a, p. 5); larva of *Necrophylus* sp., simplified after Herrera-Flórez et al., (2020, Fig. 5A, p. 311); "chimera", simplified after Haug et al., (2019a, Fig. 4, left p. 8)

stylets is not accessible, yet also this larva has very slender elongated stylets.

To a certain degree, the loss of slenderness is also recognisable in other lacewing lineages. Larvae of Myrmeleontiformia, the large group of antlion-like lacewings, often have massive, teeth-bearing stylets and broad head capsules housing massive muscles for moving these effectively (Badano & Pantaleoni, 2014a, 2014b;

Badano et al., 2017). Yet, about 100 million years ago, some myrmeleontiformian larvae had a significantly more slender appearance including more elongated appearing stylets (Badano et al., 2018, 2021; Haug et al., 2019a, 2019b, 2021a; Zippel et al., 2021). Even larvae that have been considered to appear overall similar to larvae of modern owlflies in fact have more slender appearing stylets than their modern counterparts (cf. Henry, 1976; Badano & Panteleoni, 2014b vs. Wang et al., 2016; Badano et al., 2018). Also other fossil lacewing larvae of so far unclear closer relationships have very elongated stylets with a gentle curvature (Haug et al., 2019c, 2021a).

Comparable to the discussion above, it may appear that the slender morphology represents an evolutionary ancestral one. There is a case in which a two-movable-fingers configuration evolved from elongated to stouter forms: the venom claws in centipedes (Haug et al., 2014). Yet, in centipedes basically all steps of the evolutionary transition are represented in the modern fauna, also the elongated ones. Furthermore, the ancestrally elongated morphology of the centipede venom claw results from the fact that it evolved from a walking-type leg. For the stylets of lacewing larvae, we cannot assume a similar pattern, as neither mandibles nor maxillae are especially elongated ancestrally in the groups Neuropterida (the larger group including lacewings) as demonstrated by larvae of the other major lineages, Megaloptera (Beutel & Friedrich, 2008; Bowles & Contreras-Ramos, 2016; Contreras-Ramos & Harris, 1998) and Raphidioptera (Aspöck, 2002; Aspöck & Aspöck, 2009; Aspöck et al., 1974; Beutel et al., 2014). It therefore seems most likely that the slender morphologies in the fossils do not represent an ancestrally retained morphology, but more likely a specialised one.

There is a notable exception to the general observation of "loss of slenderness". The stylets of larvae of Sisyridae (spongilla flies) are extremely slender and thin, especially in the later larval stages (recently summarised in Haug et al., 2022c). In overall shape, they resemble the long cerci of earwigs subdivided into ringlets and are, like these, not used for grasping. While the stylets of larvae of Sisyridae are not subdivided, they are in fact strongly bendable (Hamada et al., 2014, Fig. 3, p. 344; Canard et al., 2015, Fig. 2, p. 19; Notteghem, 2016, Fig. 6, pp. 137; Haug et al., 2022c, Fig. 2, p. 16), hence also in this aspect being comparable to the elongated cerci. These stylets seem not to have evolved by the Cretaceous (Haug et al., 2022c). The pattern in lacewings is, therefore, even more similar to that in earwigs: In the modern fauna, there are immatures with very thin elongated and flexible structures (cerci/stylets) and shorter more robust ones. An intermediate type of morphology of these structures being moderately elongated and slender but not flexible was present in both lineages in the Cretaceous, but is absent in the modern fauna, possibly as a result of disruptive selection (Fig. 10). This morphology was in both cases not an ancestral one, but more likely represents specialised morphologies also in both cases.

Ecological function of extinct elongated grasping structures

As we assume in both cases that the extinct morphologies represent specialisations, we need to further assume also a specific function in both cases. As discussed in Haug et al. (2019b), the rather slender head capsule in combination with the elongated stylets in some Cretaceous larvae would have provided less force when closing the stylets than the morphology of many extant larvae with broader heads and shorter stylets (see also discussion on centipede venom claws; Haug et al., 2014). We can assume the same for the cerci of earwigs. Some modern lacewing larvae hunt quite large prey (Griffiths, 1980) and this has also been observed in earwigs (Matzke & Klass, 2005, Fig. 1, p. 101). Smaller prey seems not easily handleable for modern antlion larvae (Humeau et al., 2015, p. 780). As the elongated structures (cerci/stylets) appear thinner and with this weaker and the forces produced are likely smaller, they may have been optimised for smaller prey. Yet, for earwigs we have to be aware that not all are predatory (e.g., Grimaldi & Engel, 2005, p. 217), and the cerci may have not been used in the Cretaceous earwigs for catching prey; yet, it still remains a possibility that smaller prey items were grasped by them.

A smaller prey size can explain the lower necessary forces, as well as the overall thinner appearance of the structures, but not yet the elongation. The elongation leads to weaker forces, and a smaller prey would demand weaker forces, yet that would also be possible with shorter but thin structures. It is therefore likely to have also an advantage from the elongation. Grasping prey items between the tips of the elongated structures (cerci/stylet) would create some distance between many structures of the predator and the prey. Specialisations to increase this distance are known in certain modern larvae of thread-winged lacewings (Haug et al., 2021c; Herrera-Flórez et al., 2020), but also some extinct lacewing larvae (Badano et al., 2021; Zippel et al., 2021) (Fig. 10).

Modern ecological substitutes?

As pointed out, the modern fauna lacks the specific elongated morphology of stylets of certain Cretaceous lacewing larvae and cerci of certain Cretaceous immature earwigs. Yet, the suggested ecological role as predators of smaller prey items is also realised in the modern fauna. Particularly certain lacewing larvae are specialised on smaller prey items, such as larvae of dustywings

(Coniopterygidae) and aphidlions (larvae of Chrysopidae and Hemerobiidae). Dustywing larvae are so far unknown in the Cretaceous, but are present in younger ambers; their specific morphology has possibly evolved after the Cretaceous (Haug et al., 2022c). Aphidlions (especially of the group Hemerobiidae) seem to have diversified after the Cretaceous as well (Haug et al., 2022b). It could therefore be assumed that these partly took over the extinct role represented by the elongated structures. Yet, neither larvae of dustywings nor aphidlions have structures for keeping prey at distance. It therefore seems not as a case of direct substitution. In principle, we have to assume a smaller prey back in the Cretaceous that would be more of a threat to the predator than, for example, an aphid. Until we find a case of one of these fossils with elongated structures with a prey item squeezed between them, this must remain speculative.

Conclusion

Within Euarthropoda, different types of structures have evolved specialised for grasping (e.g., prey items), among them configurations with two moveable fingers, as, e.g., in the mouthparts of aphidlion larvae or in the cerci of most earwig immatures. Comparing these grasping structures quantitatively and qualitatively reveals in both groups that some Cretaceous representatives possess elongated, slender and mildly curved structures. This morphology is not found in extant representatives of both groups. A subsequent loss of morphological diversity is observable over time in both groups, though more so within earwig immatures. The slender fossil morphology, at least in the case of the earwig immatures, plots in the morphospace area roughly in between the two very different morphologies of extant representatives, namely stout, pincer-type cerci and very elongated, subdivided cerci. The fossil slender morphology appears to be specialised and not ancestrally retained, as extant earwig immatures with very elongated cerci have stout pincer-type cerci as adults. Potentially, disruptive selection may have caused the loss of the slender fossil morphology. The ecological function of the slender morphology in both groups may have been a specialisation for smaller prey items, as elongate structures cannot exert the same forces as shorter ones. The elongation of the structures may have helped to create distance to the prey as a sort of "safety precaution". Though this specific elongated morphology is not found within insects today, there are groups within Neuroptera that are specialised on smaller prey and may have potentially replaced these fossil elongated and slender morphologies today. Especially in earwig immatures and partially also within aphidlion-like larvae there was a loss of morphological diversity over the last 100 million years and a drive for specialisation that occupies a net smaller area of the morphospace. Morphometric studies as a quantitative tool to compare a wide array of fossil and extant morphologies can help to better understand the ecological function of the fossils and their potential role within extinct food webs.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13358-023-00286-2.

Additional file 1: Table S1 Information on the specimens included in the analyses.

Additional file 2: Text S1: Additional references used in Table S1 not used in the main manuscript.

Additional file 3: Text S2: Results of the principal component analysis of the shapes of the cerci of earwigs.

Additional file 4: Text S3: Results of the principal component analysis of the shapes of the cerci of immature earwigs and the stylets of lacewing larvae.

Additional file 5: Fig. S1: Graphical representation of the factor loadings of the shape analysis of the cerci of earwigs.

Additional file 6: Fig. S2: Graphical representation of the factor loadings of the shape analysis of the cerci of immature earwigs and the stylets of lacewing larvae.

Additional file 7: Files 1–5: Files resulting from the shape analysis of the cerci of earwigs, including chain codes, aligned shapes, and principal component analysis.

Additional file 8: Files 6–10: Files resulting from the shape analysis of the cerci of immature earwigs and the stylets of lacewing larvae, including chain codes, aligned shapes, and principal component analysis.

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Author contributions

Conceptualization: CH, JTH; Methodology: CH, JTH, CK, GTH; Formal analysis and investigation: CH, GTH, CK, JTH; Writing: CH, JTH, CK, GTH; Image preparation: GTH, JTH; Funding acquisition: JTH; Resources: JTH, CH.

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Availability of data and materials

All data generated or analysed during this study are included in this published article, its figures and its supplementary files.

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